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PREY SELECTION BY THE NEOTROPICAL SPIDER *MICRATHENA SCHREIBERSI* WITH NOTES ON WEB-SITE TENACITY

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Abstract.—Prey selection and web-site tenacity are described for a population of *Micrathena schreibersi* on Barro Colorado Island, Panama. Prey selection was analyzed by first comparing web contents with insect samples obtained from sticky trap samples and by then comparing web-caught items actually being consumed with items left unattacked and uneaten. Webs exhibited no positive or negative selectivity for Coleoptera, nematocerous Diptera, or parasitoid Hymenoptera. They did, however, catch a higher proportion of ants and a lower proportion of non-nematocerous Diptera than expected from the sticky trap samples. Among items caught in the web, *M. schreibersi* fed indiscriminately upon Coleoptera, ants, non-nematocerous Diptera, and parasitoid Hymenoptera but tended to ignore nematocerous Diptera. Individuals had high web-site tenacity, and of 20 spiders monitored 15 remained in the same site for 17 days.

Prey selection by web-building spiders includes two principle components. First, webs may catch a nonrandom sample of the available prey. This deviation largely reflects differing abilities for web avoidance and escape among potential prey (Eisner et al., 1964; Turnbull, 1960; Robinson and Robinson, 1970, 1973; Olive, 1980). While numerous researchers (e.g., Bilsing, 1920; Hobby, 1930, 1940; Parmenter, 1953; Robinson and Robinson, 1970) have compliled lists of dietary items, fewer studies (e.g., Kajak, 1965; Uetz et al., 1978; Uetz and Biere, 1980; Brown, 1981) have compared web contents with potential prey in the environment. Second, among items caught in the web, the spider may then feed on preferred prey but reject unsuitable prey. Such discrimination has been observed for a variety of species and may reflect chemical or mechanical defenses of the prey (Robinson and Robinson, 1973), hunger level of the spider (Bristowe, 1941), the spider's familiarity with the prey (Turnbull, 1960), or the energetic costs associated with feeding on particular prey (Uetz and Biere, 1980).

The present study compares the web contents of *Micrathena schreibersi* (Perty) with sticky trap samples of available prey. Field work was conducted at one site over a relatively short period of time thus reducing potential complications arising from habitat and seasonal differences in prey availability. As Olive (1980) and Uetz et al. (1978) found, however, prey availability may vary over short vertical distances, and to examine this possibility potential prey were sampled at several different heights.

In addition, a second comparison was made between captured items being eaten

and those left unattacked and uneaten. Since prey ignored during the day may have been consumed at night with the web, uneaten prey did not necessarily represent rejected prey. This comparison, however, does quantify the probability of immediate attack upon different types and sizes of captured prey. While several studies (e.g., Robinson, 1969; Harwood, 1974) provide detailed descriptions of the attack and wrapping behaviors used for different prey, only Uetz and Biere (1980) have quantified attack probabilities for particular types and sizes of prey.

Materials and Methods

The study was conducted between July 31 and August 16, 1980, on Barro Colorado Island (BCI), Panama. This time period falls near the middle of a rainy season, which annually extends from late April to mid-December (Croat, 1978). The island is covered by a lowland tropical moist forest (Holdridge et al., 1971). *Micrathena schreibersi* was most abundant on the island's central plateau, and all work was conducted there.

Little is known about the biology of *M. schreibersi* despite its wide distribution throughout Central America (Chickering, 1961). Females are large and brightly colored. The mean wet weight and body length of nine adult females were 180.8 mg (SD 17.7) and 11.7 mm (SD 1.20), respectively. Dorsally, the triangular abdomen is yellow with black margins and bears 10 prominent spines of various colors (white, black, red). Females appeared to construct and tend webs during the day and consume them at night. In four nights of searching, I never saw a female or an intact web. On BCI *M. schreibersi* females are abundant only in the mid to late wet season (July to December) and are rarely found during the rest of the year (Lubin 1978). Males are smaller and less conspicuous than females and are less frequently encountered. Measurements of prey selection and web-site tenacity were made only for mature females in this study.

Flying insects were sampled at 10 different sites. At each site I implanted a 2.7 m PVC pole (diameter 25 mm) by driving 0.30 m–0.45 m of its length into the ground. Wooden rods (length 30 mm; diameter 5 mm) were then fastened to the pole at 0.3 m intervals (from 0.3 m to 2.1 m above ground). Fastened at one end, each rod projected perpendicularly from the vertical pole and hence was parallel to the ground's surface. Insects were collected on tanglefoot covered traps suspended from the wooden rods. Each trap was a 15 cm by 23 cm rectangle of 3 mm thick transparent plastic coated on both sides with tanglefoot. Insects were sampled during the day only on August 6–9. Each day the traps were set between 0800 h–0900 h, taken down between 1600 h–1700 h, and stored overnight in closed boxes. Aside from Diptera and Hymenoptera, all trapped insects were identified to order. Flies were categorized as either nematocerous or non-nematocerous, and hymenopterans were subdivided into bees and wasps, parasitoids, and winged ants. All trapped insects were measured to the nearest 0.1 mm using a dissecting microscope equipped with a disc micrometer.

Each day of the study I walked through different areas of the forest (between 0900–1630 h) and examined every web encountered. All caught items were collected and labelled as either eaten (those observed being consumed) or uneaten (those stuck in the web but not being consumed). Uneaten prey were also examined for evidence of wrapping. For each web thus sampled, the height of the spider

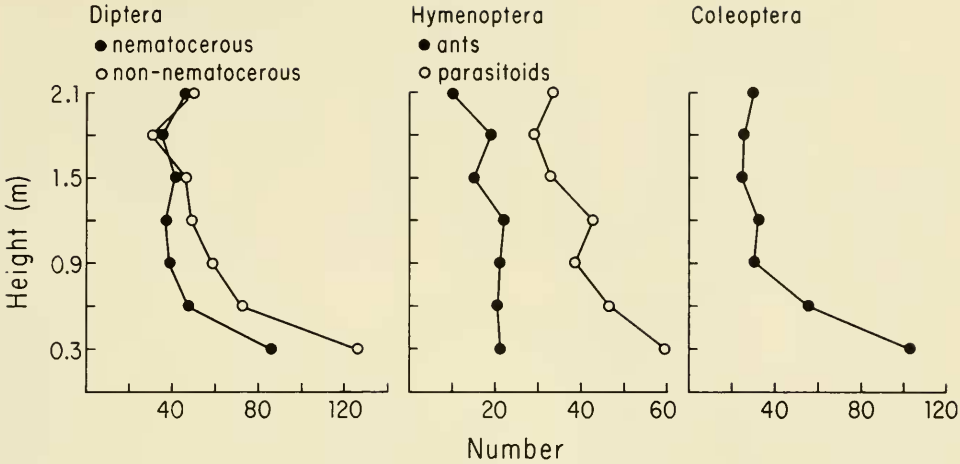

Fig. 1. Vertical distributions of the major prey categories. Each value represents the total number of individuals captured on 10 sticky traps suspended at a particular height. See text for details of sampling method.

was also recorded. Collected prey were later assigned to the appropriate prey category and measured to the nearest 0.1 mm.

Prey selectivity was quantified using Ivlev's (1961) index of electivity. Electivity (E) is calculated as follows: $E = (r_i - p_i)/(r_i + p_i)$ where r_i is the proportion of the predator's diet represented by prey type (or size class) i, and p_i is the proportion of the available prey represented by prey type (or size class) i. Values of E ranges from -1.0 (complete avoidance) to $+1.0$ (complete preference). In this study electivity values with absolute values less than 0.40 were not considered to differ from zero. (This arbitrary value was chosen primarily to facilitate discussion of the results. Ivlev's index is a descriptive measure only, and standard statistical analyses are inapplicable.) In addition, two sets of electivity values were calculated. For web selectivity (E_w) r_i is the proportion of the web contents (both eaten and uneaten items) represented by prey type i, and p_i is the proportion of available prey (as measured by the sticky traps) represented by prey type i. For spider selectivity (E_s) r_i is the proportion of the spider's observed diet (the eaten prey) represented by prey type i, and p_i is the proportion of the web contents (both eaten and uneaten items) represented by prey type i.

Results

Micrathena schreibersi generally constructed vertical webs in relatively open sections of the forest or at the edges of tree-fall gaps. Most web sites were shaded, and only rarely was a web placed in an area that received direct sunlight. Various web support structures were utilized, including leaf tips, herbaceous stems, woody vines and branches, and palm fronds. The circular webs averaged 27.4 cm in diameter and 580 cm^2 in catching area (n = 9).

Individuals may remain at a particular web-site for several weeks. On July 31 I marked the location of 20 occupied webs. These sites were then revisited daily for 17 days, and the presence or absence of the spider and the web was recorded.

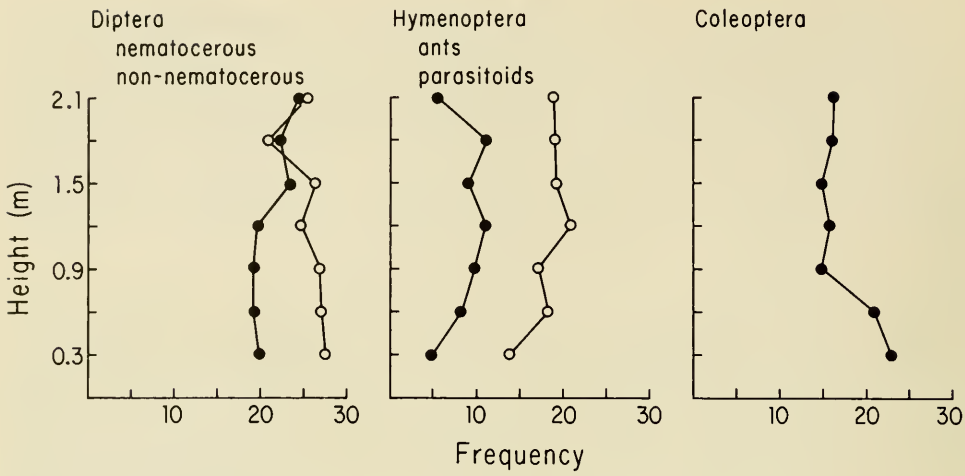

Fig. 2. Relative abundances of major prey categories over all heights sampled. Each value represents a proportion of the total number of individuals captured on 10 sticky traps suspended at a particular height. See text for details of sampling method.

In terms of the number of spiders remaining at their initial site, the results obtained were as follows: Day 1—17; Day 2 to 6—16; Days 6 to 17—15. In no instance was a spider absent but the web present; spider and web were always both present or both absent. In addition, in examining a 2 m–3 m radius about each vacated web-site, I never observed the presence of a newly constructed web.

Five prey categories comprised 89.0% of the total sample, and vertical abundance patterns were examined for these groups only. Beetles, parasitoid Hymenoptera, nematocerous and non-nematocerous Diptera all exhibited a similar trend in vertical abundance (Fig. 1). That is, the greatest numbers of individuals were collected at the two lowest sampling heights (0.3 m and 0.6 m). While similar numbers of parasitoid Hymenoptera were captured at the two lowest sampling heights, nearly twice as many beetles, nematocerous and non-nematocerous Diptera were captured at 0.3 m than 0.6 m. Ants were captured in relatively constant numbers over all sampling heights.

Although the numbers of trapped individuals varied greatly with height for four prey categories, each major category comprised a relatively constant proportion of the total sample at each height (Fig. 2). Similarly, within each category size frequency distributions did not vary with height in any obvious manner (Fig. 3). Thus, while the abundance of flying insects varied with height, the taxonomic and size composition of this fauna did not.

The vertical distribution of *M. schreibersi* did not closely match that observed for available prey (Fig. 4). *Micrathena schreibersi* preferred web-sites between 0.6 m–0.9 m, and approximately 45% of the spiders measured were within this range. Thus, while traps nearest the ground caught the greatest numbers of flying insects, only 31% of *M. schreibersi* were found below 0.6 m.

A total of 385 insects representing five orders were taken from 276 webs of *M. schreibersi*. Approximately 95% of these insects belonged to those 5 prey categories which were most abundant in the sticky trap samples. Consequently, analysis of both web and spider selectivities will focus only upon these groups. In addition,

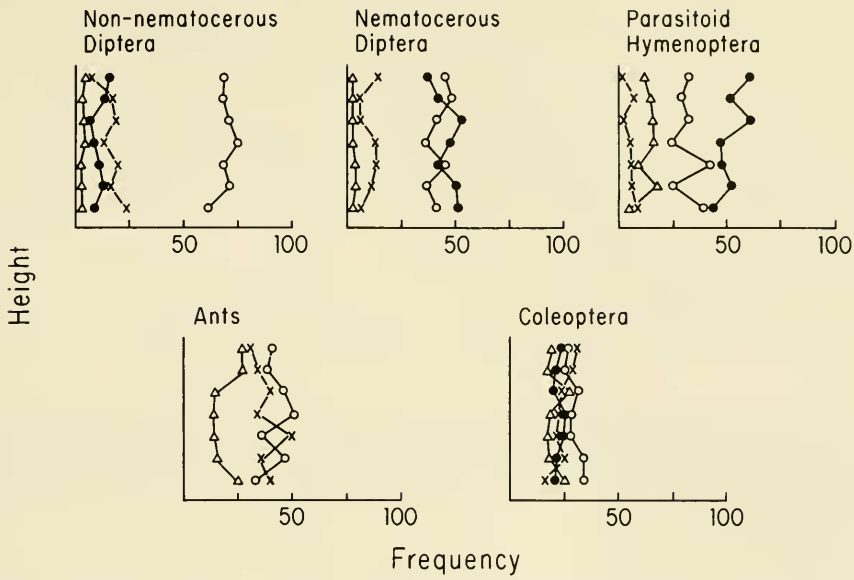

Fig. 3. Size frequency distributions for the major prey categories over the 7 heights sampled. Within a category each value represents the proportion of individuals captured at a particular height that fell within a particular 1 mm interval. The symbols used for the various size classes are: 0–1 mm (●), 1–2 mm (○), 2–3 mm (×), and >3 mm (△).

since the composition of the flying insect fauna did not much vary with height, both the data regarding prey availability and diet were combined over all heights.

Web selectivity values did not differ greatly from zero for beetles, nematocerous Diptera, or parasitoid Hymenoptera (Table 1). Ants, however, comprised a large proportion of the web contents relative to their proportion on the traps. Conversely, non-nematocerous Diptera represented a small proportion of the web contents compared to their proportion on the traps.

Only 2 groups, nematocerous Diptera and ants, were found in webs in sufficient numbers to allow meaningful calculation of web selectivity values for different size classes. Nematocerans less than 1 mm were relatively less abundant in webs than on the traps, while the opposite was true for those between 1 mm–2 mm (Table 2a). Web selectivity values, however, did not differ greatly from zero for either size class. The majority (55%) of ants in webs were 5 mm–8 mm long (Table 2b). In contrast, most (76%) ants on the sticky traps were less than 3 mm long. Consequently, web selectivity values for the 1 mm–2 mm and 2 mm–3 mm size classes were large and negative, while those for larger classes were all large and positive. Among the larger size classes, electivity values were not different from zero for 3 mm–4 mm and >8 mm but were large and positive for all remaining intervals.

Aside from nematocerous Diptera, *M. schreibersi* were observed to consume prey types in proportions roughly equal to their proportion in the web (Table 3). Spider selectivity values for beetles, ants, non-nematocerous Diptera, and parasitoid Hymenoptera were all less than 0.15 (absolute value). In contrast, the E_s value for nematocerous Diptera was large and negative. As the E_s values imply, the majority (58%) of uneaten prey were nematocerous Diptera. Most of these,

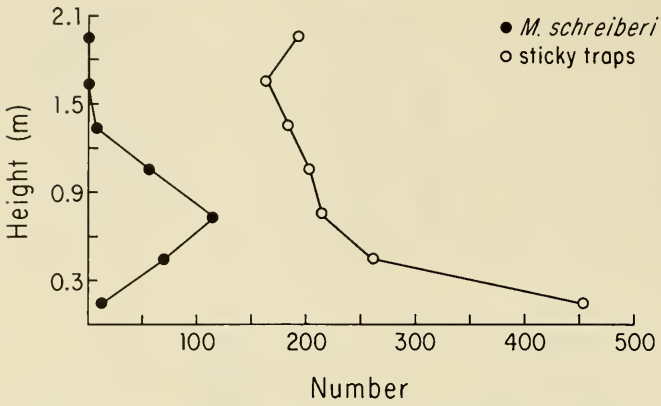

Fig. 4. Vertical distribution of *M. schreibersi* and available prey. Heights of hub-resting spiders were measured to the nearest cm and then placed into 0.3 m intervals. Values for prey represent the total number of insects captured on 10 sticky traps suspended at a particular height. See text for details of sampling method.

in turn, did not appear to have been wrapped. Many, in fact, were observed struggling in web while stuck by a single wing. In contrast, most of the other uneaten insects had clearly been attacked and wrapped.

Only ants were eaten in sufficient numbers to allow meaningful calculation of spider selectivity values for different size classes. *Micrathena schreibersi* appeared to ignore 1 mm–2 mm ants (4 eaten/18 uneaten; E = −0.65) but consume all larger size classes in proportions approximately equal to their proportions in the web. E_s values were less than 0.09 (absolute value) for all size classes >2 mm. Among the remaining groups, only beetles and nematocerous Diptera had large enough numbers of eaten and uneaten individuals to permit comparison. Mean body lengths for eaten ($\bar{x}$ = 3.9 mm; SD = 2.1) and uneaten ($\bar{x}$ = 3.4 mm; SD = 1.9) beetles were not significantly different (t = .09; P < .5). However, mean body lengths for eaten ($\bar{x}$ = 1.9 mm; SD = 1.1) and uneaten ($\bar{x}$ = 0.9 mm; SD = 0.31) nematocerans differed significantly (t = 3.9; P < .001).

Table 1. Web selectivity (E_w) values for prey types collected from webs of *M. schreibersi*.

Insects	Collected from Webs (Eaten and Uneaten)		Captured on Traps		
	No.	R_i	No.	p_i	E_w
Coleoptera	48	12.5	320	19.2	−0.21
Nematocerous Diptera	91	23.6	337	20.2	+0.08
Non-nematocerous Diptera	31	8.0	453	27.1	−0.54
Ants	170	44.1	119	7.1	+0.72
Parasitoid Hymenoptera	31	8.0	264	15.8	−0.33
Others	14*	3.6	175**	10.4	—

* Others include: Lepidoptera (4), Aculeate Hymenoptera (5), Homoptera (5).

** Others include: Lepidoptera (2), Aculeate Hymenoptera (2), Homoptera (80), Thysanoptera (27), Hemiptera (8), Orthoptera (5), Collembola (3), Zoraptera (4), Plecoptera (3), Isoptera (21), Psocoptera (20).

Table 2. Web selectivity (E_w) values for size classes of nematocerous Diptera and ants collected from webs of *M. schreibersi*.

a. Nematocerous Diptera

	Collected from Webs (Eaten and Uneaten)		Captured on Traps		
	No.	r_i	No.	p_i	E_w
0–1	27	29.7	138	40.7	−0.16
1–2	60	65.9	163	48.1	+0.16
2–3	3	3.3	31	9.1	−0.47
3	1	1.1	7	2.1	+0.31

b. Ants

	Collected from Webs (Eaten and Uneaten)		Captured on Traps		
	No.	r_i	No.	p_i	E_w
0–1	0	0.0	0	0.0	—
1–2	22	12.9	43	36.7	−0.48
2–3	17	10.0	46	39.3	−0.59
3–4	14	8.2	7	6.0	+0.15
4–5	16	9.4	3	2.6	+0.57
5–6	19	11.1	3	2.6	+0.62
6–7	49	28.8	7	6.0	+0.65
7–8	26	15.3	2	1.7	+0.80
8	7	4.1	6	5.1	−0.10

Discussion

Field studies of prey selection invariably rely upon sampling methods which yield biased estimates of both available and actual prey. The extent to which these sampling biases affect measurement of prey selection must therefore be assessed.

Sticky traps have an inherent bias resulting from the fact that different insects have different abilities to detect and avoid a trap. Although the traps used in this study were transparent, application of the tanglefoot to the plastic produced a light blue color. By rendering the trap more visible, this color may have allowed the more visually acute insects (e.g., bees, butterflies) to successfully avoid capture. Large wasps, for example, have been observed to actively avoid suspended traps (Robinson and Robinson 1973). While small insects may be less able to avoid traps, Olive (1980) has suggested that they may be passively carried around traps by air currents. This bias appeared to be unimportant for this study, however, since (1) winds were typically very light and (2) during approximately 3 h of observation I never saw an insect being passively carried around a trap.

Regarding actual prey, the "encounter and examine" method of sampling web contents is subject to a "handling time" bias. That is, small prey that are rapidly consumed are less likely to be sampled than larger items that require longer processing times. Since *M. schreibersi* catches and consumes relatively small insects, this sampling bias perhaps represented the greatest potential source of error in the study. In particular, the dietary importance of small Diptera and parasitoid Hymenoptera may have been underestimated.

Since no other sampling methods were used simultaneously, the effects of these

Table 3. Spider selectivity (E_s) values for prey types collected from webs of *M. schreibersi.*

Insects	Collected from Webs (Eaten only)		Collected from Webs (Eaten and Uneaten)		
	No.	r_i	No.	p_i	E_s
Coleoptera	30	11.8	48	12.5	−0.03
Nematocerous Diptera	16	6.3	91	23.6	−0.58
Non-nematocerous Diptera	27	10.6	31	8.0	+0.14
Ants	146	57.2	170	44.1	+0.13
Parasitoid Hymenoptera	26	10.2	31	8.0	+0.12
Others	10*	3.9	14**	3.6	—

* Others include: Lepidoptera (2), Aculeate Hymenoptera (4), Homoptera (4).
** Others include: Lepidoptera (4), Aculeate Hymenoptera (5), Homoptera (5).

potential biases could not be adjusted with correction factors (e.g., Taylor, 1962). As a result, these effects will inevitably be included in any analysis of prey selection. This notwithstanding, the present findings are believed to at least highlight some major features of the predatory behavior of *M. schreibersi.* These features were:

(1) *Micrathena schreibersi* generally remained at a particular web-site for several weeks. Interestingly, 4 of the 5 individuals that abandoned a web-site did so within the first 2 days of observation. While not conclusive, this finding suggests that these spiders had only recently selected web-sites, "sampled" them for 1 or 2 days, and then abandoned them as unfavorable. The fact that no movements were noted after Day 6 further suggests that females, once having found a suitable site, tend to remain at that site. While this interpretation is consistent with Janetos' (1982) decision rule hypothesis for web-site tenacity, residency periods noted here were much longer than those recorded for the temperate species he studied. Working with 12 orb-weaving species, Janetos (1982) found the majority of inter-movement intervals to be less than 1 day. Based largely on this finding, Janetos (1982) proposes that orb-weavers as a whole be considered active foragers which, because of low web construction costs, frequently abandon sites in search of prey "hot spots." The high site fidelity of *M. schreibersi,* however, seriously challenges the validity of this generalization.

(2) Most *M. schreibersi* did not construct their webs at heights where total prey abundance was greatest. Since the taxonomic and size composition of the flying insect fauna varied only slightly with height, *M. schreibersi* was apparently not responding to the vertical distribution of a particular type (at least at the ordinal level) or size of prey. Since a wide range of supports was used, it appears unlikely that the observed distribution reflected the distribution of a limited number of suitable web-sites. Moreover, it is unlikely that spiders near the ground were overlooked, since individuals are large and brightly colored and easily spotted in the field. Interspecific competition did not obviously inhibit use of lower web-sites, since no other species of similar size constructed webs closer to the ground (Shelly, per. obs.). High web-sites, however, may reduce risks of predation by ground-dwelling predators.

(3) Webs displayed positive selectivity for ants and negative selectivity for non-nematocerous Diptera. This result may reflect (1) the relative abilities of these prey types to avoid and/or escape webs and/or (2) placement of webs in areas

having high ant and low non-nematocerous Diptera abundances. While a rigorous assessment of these explanations is not possible, two observations suggest the former explanation to be more likely. First, I carefully searched the area (3–4 m radius) around 41 webs and never found an active ant's nest. Second, ants appeared to be less capable of escape than flies of similar size. I threw an ant (n = 15; body lengths 5–7 mm) or a horse fly (n = 15; body lengths 6.5–8 mm) into 30 different webs from which spiders had been removed. I then recorded whether or not the insect escaped within two minutes. A significantly ($t = 4.2$, $P < .001$; Sokal and Rohlf, 1969: 607) greater proportion of horse flies (47%) escaped than ants (13%).

(4) Among web-caught items, *M. schreibersi* was more likely to attack larger prey. Numerous studies (e.g., Robinson and Robinson, 1970, 1973; Riechert and Tracy, 1975; Turnbull, 1960) note rejected prey, but few studies quantify attack vs. ignore probabilities for different prey. Here, the tendency of *M. schreibersi* to ignore small ants and most nematocerous Diptera probably does not reflect avoidance but rather the inability of these small, weak-flying insects to escape or damage the web. Thus, *M. schreibersi* may have ignored these weak prey only to consume them with their web in the evening. Interestingly, the mean body length of nematocerans being consumed was approximately twice that of nematocerans caught in the web but ignored. Similar selection for larger prey has also been demonstrated for the congener *M. gracilis* (Uetz and Biere, 1980).

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